

Succession of Collembola and some ecosystem components on a pingo in the Mackenzie River Delta, N.W.T., Canada

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Received 17 August 1992

A pingo transect 5 km NE of Tununuk Point, Richards Island, N.W.T., was chosen for studies of the succession of soil Collembola, soils and vegetation. Some well established altitudinal zones of plant and collembolan communities and soil types, representing stages of different successional age, were established on the pingo and its foot-hill. A mosaic of vegetation subtypes was typical on the pingo foot-hill, whereas the older successional stages on the slope up to the pingo top formed three different vegetation belts. The soils across the transect developed from the former lake sediments and peat to Cryic Brunisol. The humus form changed during the succession in the sequence peat → raw-humus → raw-humus-moder → moder, and the clay B-horizon came closer to the soil surface. The succession of collembolan communities started with a low diversity semiaquatic community dominated by *Ceratophysella czukczorum*, *Isotoma cf. neglecta* and *Anurida decemoculata*. The species diversity was high in more advanced communities. In these, large euedaphobionts with a furca were the dominant life-form. *Folsomia bisetosa*, *F. regularis*, *F. quadrioculata*, *C. czukczorum* and *Willemia similis* appeared eudominantly in certain seral communities.

1. Introduction

The successive ecosystem development is an important ecological phenomenon. It is a long-term process usually occurring over a time span longer than the life-time of one human generation. Therefore, the methodical approach to succession studies has some difficulties, as was already pointed out by the founder of the succession theory (Clements 1916). Behind some receding glaciers are well dated plots with a different long successive development. The soil zoology was studied by Janetschek (1949) in the Austrian Alps and by Bødvarsson (1966) on Southeastern Iceland.

Pingos are geomorphological unit in the low tundra. They originate in the sediments of lakes, formerly deep enough to retain unfrozen water and underlying sediments in winter, but whose level later dropped so that they freeze to the bottom. Centripetal permafrost aggradation ensues, and the segregation and freezing of pore water results in upthrusting of the sediments to form a dome with a core of pure ice (Hyvärinen & Ritchie 1975). The distribution, origin, and growth of the pingos, abundant in the area east of the

Mackenzie Delta, have been described by Mackay (1963). The available evidence indicates that the Mackenzie pingo sediments are of late-Quaternary age, and a marked cooling of the climate 2000 to 4000 years ago might have been responsible for pingo growth (Mackay 1963). Radiocarbon analyses of two pingos, about 10 m high, in this area suggested that their growth was initiated at least 2500–3000 years ago (Hyvärinen & Ritchie 1975).

I have visited the Mackenzie Delta during the arctic summer of 1975 and studied the ecosystem zonation, especially Collembola, on a typical pingo east of the Richards Island. The goals of this contribution are to describe the collembolan communities, vegetation types and soil profiles through a pingo transect and to analyze and discuss the long-term successional patterns of these ecosystem components.

2. Material and methods

The study area was in the Mackenzie River Delta, about 5 km NE from the Tununuk Point, Richards Island, on the

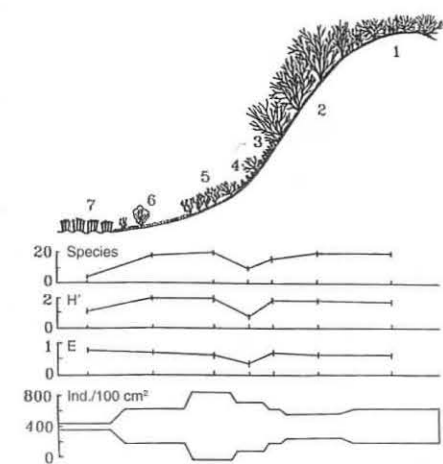


Fig. 1. Pingo transect (sites 1–7) with characteristics of the collembolan communities: no. of species, Shannon-Wiener index of diversity, evenness, and density of Collembola.

mainland about 1 km E of the Eastern Channel of the river (134°31'W, 69°03'N). The pingo was 13 m high (50 m ASL) and surrounded by a swampy bog covered with sedge and *Sphagnum* vegetation. Seven sites in a transect from the top of the pingo through the eastern slope to the sedge vegetation on the foot-hill were selected for study (Fig. 1). They represent the successively most developed ecosystem (site No. 1) on the top, the least developed ecosystem (site No. 7) and five more stages in the succession. 10 soil samples (10 cm², 5 cm deep) were taken on July 2nd, 1975 randomly on each site for soil microarthropod studies. They were transported to the laboratory in plastic bags and extracted using Tullgren funnels. Rusek's (1989) life-form classification of Collembola is used. Soil profiles were described and dominant plant species recorded on each site. Plant cover was placed into the main vegetation types following Corns (1974).

2.1. Site description

Site No. 1: Tall Shrub-Herb vegetation type on the pingo top. Plant community with dominant *Salix pulchra* (1–1.5 m tall).

Site No. 2: Tall Shrub-Herb vegetation type 5 m below the pingo top. Plant community with dominant *Salix pulchra* and *Salix lanata* ssp. *richardsoni* (1–3 m tall).

Site No. 3: Low Shrub-Herb vegetation type 8 m below the pingo top. Plant community with sparse growth of *Salix pulchra* (less than 1 m tall) and dominant *Empetrum nigrum* ssp. *hermaphroditum*.

Site No. 4: Low Shrub-Heath vegetation type 9 m below the pingo top dominated by *Arctostaphylos rubra*.

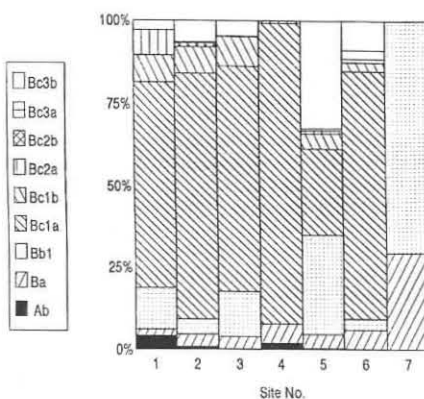


Fig. 2. Collembolan life-form structure on sites No. 1–7. Life-forms: A — atmobionts, Ab — microphytobionts, B — edaphobionts, Ba — epigeants, Bb1 — upper hemiedaphobionts, Bc1a — large euedaphobionts with furca, Bc1b — large euedaphobionts with reduced furca, Bc2a — medium euedaphobionts with furca, Bc2b — medium euedaphobionts with reduced furca, Bc3a — small euedaphobionts with furca, Bc3b — small euedaphobionts with reduced furca.

Site No. 5: Low Shrub-Heath vegetation type on the foot-hill of the pingo. Vegetation dominated by low (lower than 1 m) shrubs of *Betula glandulosa*.

Site No. 6: Low Shrub-Heath vegetation type on the foot-hill of the pingo. This is a transitional, intermediate type of vegetation to the Medium Shrub-Heath type with sparse and low shrubs of *Alnus crispa* ssp. *crispa*, *Betula glandulosa* and *Salix* sp., with dominant *Arctostaphylos rubra*, *Ledum palustre* ssp. *decumbens*, *Rubus chamaemorus*, mosses, lichens and *Sphagnum*.

Site No. 7: Herb Type vegetation. Sedge subgroup. This plant community was dominated by *Sphagnum* sp., *Eriophorum angustifolium* ssp. *triste*, *Carex rariflora* and *Carex aquatilis*. Peat (organic) soil (rests of *Sphagnum*). Standing water in the low-center polygon areas.

3. Results

3.1. Collembola

Altogether 39 species of Collembola were found in the sites along the pingo transect (Table 1). Their lowest density was in the sedge ecosystem (site No. 7), 8800 ind./m², the highest one in the low shrub-heath vegetation type with dominant dwarf birch (site No. 5), 97300 ind./m². On other sites their density was higher than 32300 ind./m² (Table 1, Fig. 1). Values of the Shannon-Wiener index of diversity (H') were lowest for sites No. 4 and 1: 0.8 and 1.1, respectively, for other sites it reached values 1.8–2.0 (Fig. 1). Evenness (E) was

lowest at site 4 ($E=0.384$), whereas they were between 0.633 and 0.811 at other sites. Site 7 had the highest E -value (Fig. 1). The lowest number of species occurred at sites No. 7 (4 spp.) and 4 (10 spp.), at other sites their number reached 16–20 (Fig. 1). The Collembola were represented by two and four life-forms in sites No. 7 and 4, respectively, at other sites they were 7–8 forms, but their proportion was different (Fig. 2). Site No. 7 was highly dominated by the upper hemiedaphobionts, whereas they were not so dominant at other sites, except No. 5. In the more developed terrestrial habitats large euedaphobionts having a furca dominated (Fig. 2). It is interesting that the medium size euedaphobionts with a reduced furca were almost absent in the succession. Some life-forms increased their species number with the successional age (Bc1b, Bc3b from site No. 3 to No. 1) (Fig. 2).

Folsomia bisetosa, *F. regularis*, *F. quadrioculata* and *Entomobrya erratica* were present in all terrestrial sites (Table 1), but their densities differed substantially. *Anurida decemoculata* only occurred in the semiaquatic sedge ecosystem, while *Folsomia* sp. n., *Hymenaphorura subtenuis* and *Anurida hammerae* occurred in the most advanced ecosystem on the pingo top (site No. 1). Some species were extremely abundant in only one site (Table 1), e.g. *Ceratophysella czukczorum* (site No. 5), *Hypogastrura macrotuberculata* (site No. 3), *Willemia similis* (site No. 5), *Folsomia bisetosa* (site No. 4). Some species occurred only up to a certain developmental stage (e.g. *Ceratophysella czukczorum*), or in a narrow belt of sites across the transect (*Arrhopalites* sp. n. — sites No. 5, 6), *Metisotoma grandiceps*, *Isotoma ekmani* (No. 4, 5), *Hymenaphorura tala* (No. 2, 3) (Table 1).

Table 1. Density (ind./100 cm²) of Collembola species in a successional row of sites (1–7) on a pingo in Mackenzie River Delta. For life-form abbreviations see Fig. 2 caption.

Life-form, species	Site:	1	2	3	4	5	6	7
Bc1a <i>Folsomia bisetosa</i> Gisin, 1953		208	44	128	489	94	96	—
Bc1a <i>Folsomia regularis</i> Hammer, 1953		60	126	78	1	131	154	—
Bb1 <i>Ceratophysella glancei</i> Hammer, 1953		38	—	—	—	—	7	—
Bc2a <i>Folsomia</i> sp. n.		30	—	—	—	—	—	—
Ab <i>Entomobrya erratica</i> Brown, 1932		18	3	1	12	4	1	—
Bc1b <i>Protaphorura macrodentata</i> (Hammer, 1953)		16	13	30	—	9	—	—
Bc3b <i>Willemia similis</i> Mills, 1934		11	19	20	—	229	—	—
Bc1b <i>Hymenaphorura subtenuis</i> (Folsom, 1917)		10	—	—	—	—	—	—
Bc1b <i>Protaphorura</i> sp.		9	—	—	—	—	—	—
Bb1 <i>Morulina thulensis</i> Hammer, 1953		8	1	—	—	—	—	—
Bb1 <i>Anurida hammerae</i> Christiansen, 1952		8	—	—	—	—	—	—
Ba <i>Sminthurinus</i> sp. juv.		3	2	—	—	1	9	—
Bc2a <i>Isotoma notabilis</i> Schaeffer, 1896		3	—	—	1	7	—	—
Ba <i>Isotoma blufusata</i> Fjellberg, 1978		3	7	—	—	24	—	—
Bc1a <i>Folsomia quadrioculata</i> (Tullberg, 1871)		2	71	91	35	28	66	—
Ba <i>Isotoma gr. viridis</i> Bourlet, 1839		2	2	—	5	2	4	—
Bc3b <i>Micranurida</i> sp.		1	2	—	—	57	27	—
Bb1 <i>Ceratophysella denticulata</i> (Bagnall, 1941)		1	12	3	—	—	—	—
Bc3b <i>Willemia anophthalma</i> Boerner, 1901		1	—	—	—	28	13	—
Bc1a <i>Isotomiella minor</i> (Schaeffer, 1896)		1	—	—	—	—	—	—
Bc1b <i>Hymenaphorura tala</i> (Christ. et Bell., 1980)		—	7	4	—	—	—	—
Bc1b <i>Protaphorura duodecimpunctata</i> (Folsom, 1919)		—	4	2	—	37	12	—
Bc2b <i>Oligaphorura affinis</i> (Agren, 1903)		—	4	1	—	—	—	—
Bc1b <i>Onychiurus</i> juv.		—	2	—	—	—	—	—
Bb1 <i>Deutonura</i> sp. n.		—	1	5	—	4	1	—
Ba <i>Isotoma alaskensis</i> Fjellberg, 1978		—	1	7	—	—	11	—
Bc3a <i>Megalothorax minimus</i> (Willem, 1900)		—	1	—	—	6	17	—
Bb1 <i>Hypogastrura macrotuberculata</i> (Hammer, 1953)		—	1	51	—	—	1	—
Ba <i>Sphaeridia pumilis</i> (Krausbauer, 1898)		—	—	9	—	11	2	—
Bc1b <i>Anurida</i> cf. <i>granaria</i> (Nicolet, 1847)		—	—	3	—	—	—	—
Bb1 <i>Ceratophysella pseudarmata</i> (Folsom, 1916)		—	—	1	—	—	—	—
Bc1a <i>Folsomia duodecimsetosa</i> Hammer, 1953		—	—	—	53	—	23	—
Ba <i>Isotoma</i> cf. <i>neglecta</i> Schaeffer, 1900		—	—	—	31	—	—	26
Bc2a <i>Isotoma ekmani</i> Fjellberg, 1977		—	—	—	3	2	—	—
Ba <i>Metisotoma grandiceps</i> (Reuter, 1891)		—	—	—	1	3	—	—
Bb1 <i>Ceratophysella czukczorum</i> Mart. et Bon., 1978		—	—	—	—	293	7	38
Bc1a <i>Arrhopalites</i> sp. n.		—	—	—	—	3	3	—
Bb1 <i>Anurida decemoculata</i> Hammer, 1953		—	—	—	—	—	—	23
Bb1 <i>Hypogastrura</i> cf. <i>perplexa</i> Christ. et Bell.		—	—	—	—	—	—	1
Total		433	323	434	631	973	454	88

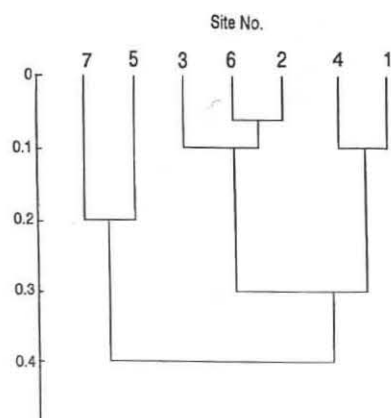


Fig. 3. Coenotical relations among the collembolan communities on sites No. 1-7 (Euclidian Distance, Word's Method, log. transformed data).

Coenotical cluster analysis (Fig. 3) has shown that the sites 7 and 5 were most different from the remaining sites, as well as from each other. Collembolan communities on sites No. 2, 6 and 3 were similar but they clustered separately from sites No. 1 and 4.

3.2. Vegetation cover

The vegetation cover was distinctly arranged into some horizontal belts (Fig. 1). A tall shrub-herb vegetation type with *Salix pulchra*, *Betula glandulosa* and *Calamagrostis canadensis* was present on the pingo top. The shrubs were only 1-1.5 m tall here. Further down a second tall shrub-herb vegetation belt dominated by *Salix lanata* spp. *richardsoni*, occurred. Here the shrubs were taller (1-3 m). Below this belt a low shrub-herb vegetation type with sparse and low *Salix pulchra* and dominant *Empetrum nigrum* ssp. *hermaphroditum* occurred. In the next belt, classified as a low shrub-heath vegetation type (sites No. 4-6), three subtypes could be distinguished. The subtype with dominant *Arctostaphylos rubra* did not form a compact belt but was distributed in a mosaic among sparse dwarf birch and willow shrubs. The subtype dominated by *Betula glandulosa* had a dense shrub cover in large or smaller patches. The third subtype, on the foot-hill of the pingo, was an intermediate type classified as a transition to a medium shrub-heath vegetation type. The semiaquatic habitat of herb-sedge type surrounded the pingo in a wide, flat area on the bottom of a former lake.

There was a mosaic of vegetation subtypes on the pingo foot-hill, whereas on the slope up to the top three well formed vegetation belts were developed. The plant cover on

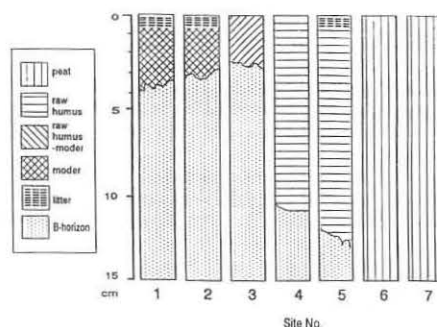


Fig. 4. Soil profiles on sites No. 1-7.

the foot-hill was successively less advanced than on the slopes and the pingo top. The lower willow growth on the pingo top was probably caused by the hill-top phenomenon.

3.3. Soils

Across the transect, the soils developed from the former lake sediment and the peat. The *Sphagnum* and peat rests reached the soil surface (sites No. 7, 6) and they represented the starting point of the terrestrial soil development. Sites No. 4 and 5, where the A-horizon was formed by raw-humus without and with litter represented the next successional stage (Fig. 4). In the following stage (site No. 3) the humus form was a transition from raw-humus to moder. The climax soil was represented by Cryic Brunisol (sites No. 1, 2) with 0.5 cm litter layer and well developed moder humus form. During the successive soil development the A-horizon lost its thickness and changed its humus form in a sequence: peat → raw-humus → raw-humus-modier → moder, and the clayic B-horizon came closer to the soil surface (Fig. 4).

4. Discussion

There are some data about the *Collembola* in pingo soils of the Mackenzie Delta area, but the investigations did not deal with succession and zonation, and the species identification is doubtful (Tanno & Shimada 1978, Toda & Tanno 1983).

During the pingo growth the top was the first part emerging from the water environment and the successive development to terrestrial ecosystems started from it. During the last 2500-3000 years, closed belts of the shrubby vegetation developed on the upper pingo part, whereas, on the foot-hill successively less advanced and younger, patchily distributed plant communities occur. The soil profiles show similar developmental patterns. Soils without and with well differentiated litter layer occur on the foot-hill, but a litter layer is always present in the closed shrubby belts in the upper parts of the pingo and it is possible to describe a

successive sequence of humus forms along the transect from peat and raw-humus to moder.

The coenotical cluster analysis has shown, that there were more well differentiated collembolan communities than the number of main vegetation types (Corns 1974) across the transect. This was due to the lack of more detailed plant sociological studies. The density and occurrence of most *Collembola* in different sites did not show any clear successive increase or decrease. From the density distribution of some *Folsomia*-species, *Willemia similis*, *Ceratophysella czukczorum* and others (Table 1) it can be speculated that competitive relations among different species substantially control the succession. The missing Tullbergiinae and *Friesea*-species are another conspicuous feature of this succession. These species are present in other, well drained soils, in the Mackenzie Delta area. Their absence is probably connected with the pingo isolation from the surrounding terrestrial ecosystems by the aquatic and swampy areas.

The complexity of the ecosystem succession was shown on soil profile, plant cover and soil animal community development. The patterns in the succession of individual ecosystem components show a general trend of development from the semiaquatic ecosystems, across the terrestrial ecosystems on the foot-hill, to the most advanced and oldest ecosystems on the slope and pingo top. Site No. 4 does not follow the general pattern and exhibits substantially lower values of diversity, evenness and species richness of *Collembola*. Also the collembolan life-form structure was quite different from other sites (Fig. 2). The extraordinary structure of this site is difficult to explain.

Acknowledgements. I am very grateful to Prof. Dr. L. C. Bliss, Seattle, Prof. Dr. T. F. Cook, Edmonton, and Mr. R. M.

Hill, Inuvik for assistance with the trip to the Mackenzie River Delta, and Dr. T. Bolger, Dublin, for improving the English. The material for this study was collected while the author held a National Research Council of Canada postdoctoral fellowship at the Pacific Forest Research Centre, Victoria, B.C., 1975.

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